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REVIEW OF FIVE YEARS OF STUDIES
ON PHYTOPLANKTON AT SOUTHERN
CALIFORNIA PIERS, 1920-1924 INCLUSIVE

BY
WINFRED EMORY ALLEN

BULLETIN OF THE SCRIPPS INSTITUTION OF OCEANOGRAPHY
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HISTORICAL STATEMENT

Because of dissatisfaction with usual methods of plankton collecting considerable experiment was undertaken at the Scripps Institution in 1919 which resulted in the adoption in September of the method of dipping, measuring, and filtering through No. 25 Dufour bolting silk (average diameter of mesh about .05 mm.) of the samples of water to be studied. The surprising success of a method so simple and easy led to its application to another station at Pt. Hueneme (about one hundred and twenty-five miles northward) in the following January. In January, 1921, Oceanside was added as a regular station. Short series were taken at Redondo and Santa Barbara piers in 1921 but no regular stations were established there because of failure to make suitable arrangements for daily collecting. In lack of a pier at Pacific Grove the collecting undertaken there in 1923 was done by wading out a few yards in the water. At this station there was considerable discontinuity in the work.

All of the laboratory study has been done by the present writer or under his direct supervision. Computations of the numbers per liter have been made from the records of enumerations of dinoflagellates and diatoms in measured fractions of each catch. All enumerations were made by use of the Sedgwick-Rafter counting cell and the Whipple ocular disk micrometer. (Cf. Allen, 1922*a, b*, 1927*a, b*, and Dorman, 1927.)

GENERAL REMARKS

Since dinoflagellates were generally less abundant than diatoms and also less continuously represented they are given less attention in this five years' review. In the main the two groups will be discussed separately, beginning with the diatoms. For more detailed information concerning distribution of both groups see preceding reports (Allen, 1922*a, b*, 1927*a, b*, Dorman, 1927) and the report for 1924 (1928*b*). Since La Jolla and Pt. Hueneme are the only stations studied over the full period of five years they will necessarily constitute the basis for all discussion.

TABLE 1
TOTAL NUMBERS OF DIATOMS IN EACH QUARTER OF EACH YEAR, IN EACH QUARTER FOR FOUR YEARS COMBINED, AND IN EACH YEAR AS A WHOLE. ESTIMATED FROM WEEKLY AVERAGES

Station	Quarter	1920	1921	1922	1923	1924	4 years
La Jolla.....	1	938,687	582,720	161,874	281,814	32,956	1,059,364
	2	942,287	2,448,524	1,490,940	786,544	78,936	4,804,944
	3	658,085	179,489	26,648	82,474	180,412	489,023
	4	91,409	37,131	377,162	118,560	405,520	938,373
	Total.....	2,630,468	3,247,864	2,056,624	1,269,392	697,824	
Oceanside.....	1		470,356	41,208	777,103	36,672	1,325,359
	2		1,212,397	820,328	595,250	277,968	2,905,943
	3		241,031	5,476	40,256	108,384	366,147
	4		47,587	183,656	57,024	143,056	431,323
	Total.....		1,971,371	1,050,668	1,469,633	566,080	
Pt. Hueneme.....	1	126,073	505,185	40,010	555,137	132,032	1,232,364
	2	855,295	394,868	460,034	1,820,646	4,247,600	6,923,148
	3	551,425	42,715	410,296	723,260	1,329,656	2,505,927
	4	78,540	13,114	99,504	23,552	113,648	249,818
	Total.....	1,611,333	955,882	1,009,844	3,122,303	5,822,936	
RANK OF QUARTERS IN PRODUCTION EACH YEAR AS SHOWN ABOVE							
Rank of quarters in production each year as shown above.....	1	L-0-H	L-0-H	L-0-H	L-0-H	L-0-H	L-0-H
	2	2-0-3	2-2-1	3-3-4	2-1-3	4-4-3	2-2-3
	3	1-0-1	1-1-2	1-1-1	1-2-1	3-1-1	1-1-1
	4	3-0-2	3-3-3	4-4-2	4-4-2	2-3-2	4-4-2
		4-0-4	4-4-4	2-2-3	3-3-4	1-2-4	3-3-4

DIATOMS

TOTAL NUMBERS IN THE FIVE YEARS

As indicated by table 1 the total number of diatom cells at Pt. Hueneme for the five years was more than one-fourth greater than the total at La Jolla. In the quadrennium which includes Oceanside the disparity is still larger and Oceanside is considerably outnumbered by both of the other stations. The preponderance of Pt. Hueneme over the more southerly stations is mainly due to the exceptionally large numbers of 1924, the poorest year for both of the southerly stations but by far the best for Pt. Hueneme (table 1 and figs. 2 and 3). Offshore catches by boat in 1924 (Sleggs, 1927) agree with the catches of La Jolla and Oceanside piers in showing small numbers of both diatoms and dinoflagellates. Therefore, there is ground for inference that the Gulf of Santa Catalina in general presented rather unfavorable conditions. No offshore records are available for 1924 near Pt. Hueneme, but the long sustained productivity at the pier (fig. 2 and table 1) suggests the probability that conditions in the general region were favorable.

At any rate the gross indications afforded by table 1 and figure 2 make it clear that the geographic lead in numerical dominance was not suddenly acquired or confined to 1924. In 1923 the numbers at Pt. Hueneme were distinctly superior and the superiority was sustained over a considerable period. Furthermore, La Jolla shows a steady decline in numbers after 1921, while Pt. Hueneme shows almost as steady increase, Oceanside being more vacillating. The complete reversal of numerical leadership of the two stations occurring so gradually over a four-year period presents a number of fascinating problems. There is nothing in the records of temperatures and salinities (fig. 2) which offers a satisfactory basis for explanation. In fact the changes in salinity are in the same general direction at all three stations, toward a greater uniformity and slightly higher average.

SEASONAL DISTRIBUTION THROUGH FIVE YEARS

Although, as just indicated, the gross features of geographical distribution through the five years at the pier stations are confusing and, apparently, contradictory, this is not true of the seasonal distribution through the period (table 1 and figs. 3 and 4). For convenience in study and also because they correspond closely with actual

seasonal changes in the southern California region the four quarters of the year are treated as seasons in this discussion. The first thirteen weeks may be considered the Winter season followed by Spring, Summer, and Fall.

Examining first the ranking of the four quarters as shown in the last section of table 1 it appears that in eleven cases out of fourteen, second quarters held first rank in numbers produced. As shown by figure 3 one of the three failures to attain maximum numbers in the second quarter was due to the maximum weekly average for the year at Pt. Hueneme in 1921 appearing in the thirteenth week. It is also shown that another failure was due to the maximum weekly average at Oceanside falling on the eleventh week in 1923. In each of these cases the difference in time was not great enough to carry much weight in comparing productivity of the different quarters (seasons) of the year. The other exception was at La Jolla in 1924 where the maximum production of the year was reached after steady increase in each quarter to the fourth quarter (table 1). There is no doubt that this constitutes a true exception, an exception which does not forbid a conclusion that normal productivity in southern California waters is greatest in the second quarter, but which does show that even such a strong tendency as this may be nullified and the periodicity reversed in some year.

The number of weeks with average numbers above one hundred thousand diatom cells to the liter also gives strong evidence that the second quarter is the normally most productive season for diatoms. Out of seventy-eight weeks at the three stations in the five years which yielded more than that amount forty-two were in the second quarter (fig. 4). Comparison of the total numbers for the different quarters at the three stations for four years gives still further confirmation of the greater productivity of the second quarter.

The rank of the other quarters is not so distinctly indicated, although there is no real doubt that the fourth quarter holds the lowest place since it had smallest aggregate numbers in seven times out of fourteen (table 1). However, four of these times were at Pt. Hueneme, which was also the only station at which the totals for each quarter for five years indicated the fourth quarter to be much poorer than the other three. At both La Jolla and Oceanside the totals for the third and fourth quarters differed by less than ten per cent, the fourth quarter being poorest at La Jolla and the third quarter poorest at Oceanside. The constancy of the low rank of the fourth quarter at Pt. Hueneme constitutes a geographic difference between that station and the others which is fairly well defined and which deserves further attention as opportunity offers.

The distribution of maxima and minima of weekly averages and of weeks exceeding averages of one hundred thousand or falling below averages of five hundred cells to the liter (fig. 4) is also informative concerning this tendency to minimal production in the fourth quarter. In only five weeks of the aggregate of one hundred and eighty-two of this quarter at the three stations did the average exceed one hundred thousand cells to the liter, and four of these weeks were at La Jolla, the other one at Oceanside. In a similar number of weeks of the first quarter there were thirteen having averages in excess of one hundred thousand. The showing of lightly productive weeks is still more impressive, fifty-three out of one hundred and eighty-two weeks in the fourth quarter yielding averages less than five hundred cells to the liter while only twenty weeks had as low averages in the first quarter. In regard to these features the showing of the third quarter is intermediate to the other two, a condition indicated by the discussion in the preceding paragraph.

On the general showing of the quadrennial totals for the different quarters at the three stations the first quarter ranks second. Here again there is evidence of a geographic difference, Pt. Hueneme showing the first quarter in third rank while the third quarter ranked second there.

Summarizing the seasonal differences from the geographic viewpoint it may be noted that all three stations agree in having the normal season of maximum production in the second quarter, but that Pt. Hueneme differs from the other two by the distinctness of the showing of minimal production in the fourth quarter and by showing the first quarter to be plainly in third rank, whereas La Jolla and Oceanside agree in having the first quarter in second rank and in showing little difference between the third and fourth quarters. Stated in another way, La Jolla and Oceanside seem to offer better conditions for diatoms in the first half-year while Pt. Hueneme seems to offer best conditions in the half-year comprising the second and third quarters. In terms of the most obvious conditions Pt. Hueneme is least productive of photosynthetic organisms in the half-year which is most turbulent in Santa Barbara Channel. In the less turbulent waters of the southern half of the Gulf of Santa Catalina it appears that seasonal conditions are much less clearly marked and, as a consequence, maximum numbers for the year might be produced in any quarter. But that this trend in the different localities does not constitute a rule is shown (table 1) by Pt. Hueneme in 1921 when the largest numbers came in the first quarter and the numbers became successively smaller through the other three quarters.

TABLE 2
LEADING SPECIES OF DIATOMS IN EACH QUARTER OF THE YEAR

Station	Season	1920	1921	1922	1923	1924
La Jolla...	1	Nitzschia seriata.....	Chaetoceras scolopendra	Chaetoceras curvisetum.	Chaetoceras spp.....	Asterionella japonica
	2	C. curvisetum.....	C. compressum.....	C. debile.....	C. compressum.....	C. spp.
	3	C. spp.....	C. spp.....	C. spp.....	C. spp.....	C. debile
	4	Skeletonema costatum	C. spp.....	Eucampia zoodiacus.....	C. spp.....	C. curvisetum
Oceanside	1		C. spp.....	Nitzschia seriata.....	Asterionella japonica.	C. curvisetum
	2		C. debile	C. debile.....	C. spp.....	C. curvisetum
	3		C. spp.....	Navicula spp.....	C. spp.....	C. spp.
	4		C. spp.....	C. compressum.....	C. spp.....	C. curvisetum
Pt. Huenehme	1	C. debile.....	C. debile.....	Thalassiosira decipiens..	C. compressum.....	C. spp.
	2	C. affine.....	C. debile.....	C. debile.....	Nitzschia seriata.....	C. sociale
	3	Nitzschia seriata.....	C. spp.....	C. scolopendra.....	C. spp.....	C. sociale
	4	C. spp.....	C. spp.....	Nitzschia seriata.....	C. spp.....	C. debile

SEASONAL DIFFERENCES IN SPECIES NUMERICALLY DOMINANT

In view of the number of species recorded in the southern California region, nearly one hundred, it is surprising that in the five years at two stations and four years at three stations so few species and genera should be able to show numerical dominance for a quarter, considered as a unit period. According to table 2 only thirteen species groups, including ten well defined species, attained such dominance. Of the seven genera represented by this list one, *Chaetoceras*, has held the field against almost all others. This is so strongly evident that there seems to be good reason for thinking that the southern California region, and especially the Gulf of Santa Catalina, gives exceptional opportunity for the development of that group.

On account of the outstanding prominence of *Chaetoceras* discussion of seasonal distribution of the leading species is practically limited to that genus, species of other genera leading in so few quarters as to give no basis of discussion for a time unit of this magnitude. Referring again to table 2, it is fairly clear that *C. spp.* may keep the lead in any quarter, a condition which is not surprising in consideration of the mixed character of the poorly defined forms listed under this designation. The separation of *C. curvisetum* Cl. has been unsatisfactory, but whatever difference led to use of that name was found slightly more often in the first and fourth quarters than in the middle quarters. The reverse was true of *C. debile*.

Viewing unit periods of thirteen weeks as wholes there is not much indication that the seasons are strongly influential in determining the numerical leadership of particular species in the southern California region. Apparently smaller time units are necessary to show existence of such a relationship.

With months as units the list of leading species is not greatly different from that for quarters as units (cf. tables 2 and 3) but there is a little more definite indication of a tendency for certain species to take the lead in numbers at particular seasons. *Asterionella japonica* Cl., *Chaetoceras compressum*, Laud., *C. curvisetum* Cl., *C. debile* Cl., and *Nitzschia seriata* Cl. are species which seem to be somewhat more favored than others by conditions in the first half-year. Most of these same species took a considerable part in the dominance of the second half-year but less frequently. Amongst the smaller and less robust populations of the second half-year, *Chaetoceras* spp. frequently held the lead, as might be expected from the fact that this group contains a considerable number of atypical specimens which are certainly much more prominent, relatively, in periods of inferior productivity.

Numerical dominance for a month of species rarely attaining to that prominence may occur in any season of the year, but it usually occurs in months when the total number of diatoms is inferior or the commonly dominant species below their maxima for the year (table 3).

A general survey of manuscript tables too voluminous for publication indicates that, except in poorly productive periods, a very distinct difference in numbers from month to month is more often than not accompanied by a change in the leading species. When a species holds the lead for two or more months there may be either an increase or decrease in the successive months. Sometimes two species alternate in leadership two or three times. More often there is a change to a third species when the numerical dominance is broken, after one or two changes. These successional relationships of different species are even more strongly exhibited by extensive manuscript tables showing numerical dominance of species in each week of the five years. However, there is no apparent indication that the abundance of any species gives ground for predicting that it will be followed or replaced by any certain other species.

RELATION OF NUMBER OF DIATOMS TO NUMBER OF DINOFLAGELLATES

In my preliminary paper covering the catches at twelve-hour intervals at the Scripps Institution pier through the last four months of 1919 (Allen, 1921) I called attention to certain reasons for thinking that increase in size of catches of diatoms was likely to be accompanied by decreases in size of catches of dinoflagellates, and conversely. Examination of the records of weekly averages for five years does not disclose evidence to sustain that view. In general these records indicate that there is no relationship of that sort, inasmuch as the two groups often show increases and decreases at the same times, though not of similar magnitude. However, it should be apparent that the question is not settled, because no one can justly say that results of averaging daily catches for a week are comparable with the record of individual catches made at intervals of twelve hours. Theoretically, it seems probable that both things may be true and that in thin populations the two groups may respond either together or diversely to any added stimulus, but that when one group has gained a considerable advantage it may continue rapid increase with more or less detriment to the other. As a matter of fact, there is no evidence to indicate that such relationships between species of diatoms and dinoflagellates are essentially different from those between many of the associated species of either group alone.

TABLE 3
LEADING SPECIES OF DIATOMS IN DIFFERENT MONTHS

	1920	1921	1922	1923	1924
<i>La Jolla</i>					
Jan.....	Chaetoceras curvisetum	Chaetoceras spp.	Asterionella japonica	Chaetoceras spp.	Lauderia borealis
Feb.....	Nitzschia seriata	Skeletonema costatum	C. debile	C. spp.	C. scolopendra
March.....	N. seriata	C. scolopendra	C. curvisetum	C. spp.	Asterionella japonica
April.....	C. curvisetum	C. spp.	C. debile	Leptocylindrus danicus	C. compressum
May.....	N. seriata	N. seriata	C. compressum	C. compressum	Bacteriastrium varians
June.....	C. curvisetum	C. compressum	C. spp.	N. seriata	C. spp.
July.....	C. curvisetum	C. spp.	Leptocylindrus danicus	C. spp.	C. spp.
Aug.....	C. spp.	C. spp.	C. spp.	C. spp.	C. debile
Sept.....	C. spp.	C. spp.	C. spp.	C. spp.	Bacteriastrium varians
Oct.....	Dactyliosolen tenuis	C. spp.	C. spp.	C. spp.	C. curvisetum
Nov.....	C. spp.	C. spp.	Eucampia zoodiacus	C. spp.	C. sociale
Dec.....	C. spp.	C. spp.	C. compressum	C. sociale	
<i>Oceanside</i>					
Jan.....	C. spp.	C. spp.	C. didymum	Asterionella japonica	C. sociale
Feb.....	Skeletonema costatum	Skeletonema costatum	C. debile	C. spp.	C. curvisetum
March.....	C. spp.	C. spp.	Nitzschia seriata	A. japonica	A. japonica
April.....	C. debile	C. debile	C. debile	C. spp.	C. curvisetum
May.....	Leptocylindrus danicus	Leptocylindrus danicus	Thalassiothrix longissima	C. spp.	Biddulphia extensa
June.....	C. spp.	C. spp.	C. spp.	Concinnodiscus spp.	Eucampia zoodiacus
July.....	C. spp.	C. spp.	Navicula spp.	C. spp.	Rhizosolenia semispina

TABLE 3—(Continued)

	1920	1921	1922	1923	1924
<i>Oceanside—(Continued)</i>					
Aug.....		C. spp.....	Navicula spp.....	C. spp.....	R. semispina
Sept.....		C. spp.....	C. spp.....	C. spp.....	C. spp.
Oct.....		C. spp.....	C. decipiens.....	C. spp.....	C. curvisetum
Nov.....		C. spp.....	C. compressum.....	Coscinodiscus spp.....	C. spp.
Dec.....		C. spp.....	Coscinodiscus spp.....	C. spp.....	C. debile
<i>Pt. Hueneme</i>					
Jan.....		C. debile.....	C. sociale.....	C. spp.....	C. debile
Feb.....	C. debile.....	C. debile.....	C. spp.....	Skeletonema costatum.....	C. curvisetum
March.....	C. debile.....	C. debile.....	Thalassiosira decipiens.....	C. compressum.....	C. spp.
April.....	Thalassiosira decipiens.....	C. debile.....	C. debile.....	C. spp.....	C. sociale
May.....	N. seriata.....	C. spp.....	N. seriata.....	C. compressum.....	Detonula schroederii
June.....	N. seriata.....	C. spp.....	C. spp.....	N. seriata.....	C. sociale
July.....	Eucampia zoodiacus.....	C. spp.....	C. spp.....	C. spp.....	C. curvisetum
Aug.....	C. debile.....	N. seriata.....	Skeletonema costatum.....	C. spp.....	C. sociale
Sept.....	C. spp.....	C. spp.....	N. seriata.....	C. compressum.....	C. spp.
Oct.....	C. spp.....	C. spp.....	C. spp.....	C. spp.....	C. debile
Nov.....	C. spp.....	C. spp.....	C. debile.....	C. spp.....	C. debile
Dec.....	C. spp.....	C. spp.....	Biddulphia spp.....	C. spp.....	C. debile

RELATION OF DIATOMS TO ANIMALS

It is well known and by different investigators has been shown in detail that many marine animals, both free-swimming and sedentary, depend largely upon diatoms for food. Equally important, though less frequently and prominently mentioned is the fact that marine animals contribute largely, through their metabolic wastes and the products of decay, to the sustenance of marine diatoms. One of the prime objects of the high continuity and daily frequency of our collecting at pier stations has been to accumulate data which may eventually be useful in tracing the influence of these reciprocal relationships.

It is true that such interrelationships cannot be traced with full confidence and satisfaction until we have coordinated studies of animal types carried coincidentally with those of diatoms, and characterized by similar continuity, but it is also true that the continuous series now in operation, taken with the coincident hydrographic studies, constitute a solid foundation or base of reference upon which to build more general investigations.

The Scripps Institution was unable, in this five-year period, to carry continuously any kind of animal studies comparable with these studies of the diatoms. However, for a large part of one year studies of microzooplankton were conducted at the Scripps Institution pier in the same way as those of the phytoplankton (Murphy, 1924) and there is something of interest in the reports of the sardine fishery in the San Diego region in these years.

The conclusion of primary interest in Murphy's (1924) report is that the microzooplankton, and especially the copepods, tend to be abundant when diatoms are few, or at least not abundant, and that it is scanty at times of great abundance of diatoms. Of course, the evidence from a single year at a single station is not conclusive in this kind of problem, but this evidence agrees with similar evidence from other sources and it probably represents a common condition. Still such alternation of abundance is not proved and it is not safe to assume that it is the typical condition until the component populations have been carefully compared over a period of years.

If it really is the normal relationship one may suppose that the alternation may be due partly to the fact that increasing abundance of animals would result in reduction of the plants by consumption, and partly to the fact that reduction in numbers of animals gives plants opportunity to recuperate and to make use of the increased fertility of the water due to accumulation of animal wastes. It is also true that a large percentage of the microzooplankton does not use

diatoms directly for food and that the differences in abundance may be due to differences in responsiveness of these organisms to particular environmental conditions. Furthermore, it is possible that the periodicity of diatom feeders in the microzooplankton is adjusted so as to get most advantage from the diatoms by having some particular phase of the life cycle coincident with diatom abundance and another phase, numerically superior, coincident with diatom lack of abundance. The reality of such relationships can be fully determined only by careful attention to life histories as well as to changes in numbers or to changes in mass production.

Concerning the relationship of the numbers of diatoms to the numbers of sardines in the five years there is no information suitable for direct application to the questions involved. It is none the less interesting to note that 1920, next to the most productive year for diatoms at La Jolla and the year in which diatom abundance appeared earliest and held steadiest (fig. 2), was officially reported as one of the best, if not the best, of the five years for the sardine fishery. Even more interesting is the fact that from 1918 to 1920 many more sardines were seen around the Scripps Institution pier than have been seen there since that time. It is also true that complaints of San Diego commercial fishermen about scarcity of sardines were not heard in 1920 and 1921, although they have been frequent in succeeding years. While such things do not furnish an adequate basis for a definite conclusion they warrant a suggestion that the smaller numbers of diatoms and of sardines in the San Diego region for several years after 1920 may have had causal interrelationships which might have been traced if properly coordinated methods of observation could have been applied.

The years 1919, 1920, and 1921 were good ones for mackerel fishing by hook and line from the Scripps Institution pier, 1919 being best, 1920 almost as good, but 1921 notably poorer. In 1919 scores of people caught enough mackerel between August and December to salt down for winter use. Some were able to supply several families. While tow net collections of microplankton in 1919 and preceding years have not been studied in detail I had gained from them the impression that diatom production in the San Diego region had been good from the flood year of 1916 (when January rains were so heavy as to cause destruction of nearly all bridges between San Diego and Los Angeles) up to the time of detailed studies in 1919. When pier catches of 1922 yielded poorly both in diatoms and mackerel I wondered if there were a recognizable relationship between decreases of the two organisms. Lack of favorable (in time and quantity) run-off of materials from the land might prevent development of diatoms at the time necessary

to produce food for young mackerel, and the failure of these to thrive would certainly, in some following year, result in smaller numbers of a size attractive to fishermen. So far I have not been able to trace such a relationship, and the increasing interference with run-off through impounding reservoirs and other human devices makes me doubt the possibility of ever being able to trace such a relationship in this region.

I have given more attention to these points than the evidence seems to warrant partly because they illustrate strongly the difficulty of interpreting natural conditions in the face of uncertainty concerning the location of the limits of man's influence, direct or indirect.

FLUCTUATIONS IN DISTRIBUTION

Any significant discussion of distribution necessarily includes fluctuations (as indicated by preceding portions of this paper) but it is desirable also to give direct attention to particular aspects of fluctuations as illustrated in this five-year period.

In the first place it ought to be understood that the size of the units used in discussing fluctuations has a highly important relation to views of their significance and to their reliability in estimating the degree of normality of natural phenomena.

Numerous fluctuations are strongly indicated in the tables and in reports for single years, which are totally obscured in the larger units of table 1 and in figures 2 and 3. My reports for 1919 and 1920 (Allen, 1922*a*, *b*) show that still smaller units than those just mentioned exhibit far more numerous points of fluctuation, all of which are important in trying to understand causes and origins of observed conditions.

Not only have the time units been large in most of the series of plankton studies but so also have been the population units. For the most part necessity has dictated that discussion should deal with totals of diatoms and dinoflagellates with little attention to the species composing these totals. Yet it should be obvious from examination of figures 2, 3, and 4, and from comment on species components in 1924 in the forthcoming report for that year, that one gets very little comprehension of the conditions involved in the extreme fluctuations observable in that year through use of the larger units alone. But if this be true of extreme fluctuations it is doubtless even more strongly true of many moderate fluctuations. Therefore, it is probable that numerous failures to identify correlations or to catch the significance of certain fluctuations are due to use of units of too great

magnitude. The larger the units the more diffused their significance and the greater the need of caution in discussing fluctuations indicated by them.

In the second place the records accumulated in the five years show again and again that fluctuations of concurrent phenomena are inter-related to an indeterminable extent. For this reason alone attempts to designate a single "determining factor" in the causation of a fluctuation or a set of fluctuations are hazardous.

Both of these aspects of the general problem of reaching adequate understanding of fluctuations are well illustrated in the early period of high productivity of diatoms at La Jolla pier in 1920 (figs. 2, 3, 4, and 5). Figure 2, with month and total diatom units, shows merely that there was notable abundance of diatoms in February. There is no information concerning the number of species participating in this abundance and there is nothing to show what fractional part of the month produced the unusual numbers. Figure 4 makes it clearer that production was not evenly distributed over the month, but in figure 5 there is far more clarifying information.

Even this can be supplemented by a little use of manuscript tables because it happened that on January 29 (a day of very scant production of diatoms) catches were taken at hour intervals from 7 A.M. to 10 P.M. The records for this day show that both the number of diatoms and the number of species of diatoms was larger in the early forenoon than later in the day and that out of sixteen catches *Nitzschia seriata* Cl. was found present in only six, mostly in the forenoon.

NITZSCHIA SERIATA Cleve

On January 30 this species showed nearly four hundred cells to the liter in the catch at 8 A.M. and nearly two thousand at 8 P.M. A further increase occurred on January 31, after which there was no catch of *N. seriata* (either morning or evening) less than ten thousand cells to the liter for forty-five days. Figure 5 shows the fluctuations of numbers of this species at twelve-hour intervals for the forty-five days. For comparison the fluctuations in numbers of total diatoms in the morning catches is also shown. Morning and evening catches of *N. seriata* are run parallel instead of consecutively in the graph in order to show most clearly both difference in numbers at the two times of day and the strong similarity of the daily fluctuations at the two times.

Two prominent features of the fluctuations through this period would have been entirely obscured by units even so small as the day, i.e., that in thirty-two out of forty-five days the fluctuations of morn-

ing and evening catches were in the same direction, and that in thirty-four out of forty-five days the morning catches were larger than those of the evening.

It so happens in this case that the polygon of distribution for forty-five days would have approximately the same form by use of week units that it has with the day units, although it would be somewhat misleading because the highest peak of the final pulse falls in the week of less abundance, whereby it would give the impression of an approach to uniformity of distribution through the last two weeks.

But in the main the week unit would show three important features fairly well: first, the rise in abundance of *N. seriata* in one week followed by a fall in the next, a greater rise in the third, and a lesser fall in the fourth, the succeeding two weeks failing to show the actual condition. Second, the strong rise in total diatoms for one week, followed by a fall in the next week, a rise in the third, a fall in the next two, and a rise in the last. Third, the most striking point of all, that except for ten days at the first of the forty-five and seven at the last, *Nitzschia seriata* Cl. constituted nearly the whole diatom population. However, all these points are much more impressive as they appear in figure 5 than they would be in a graph using the week unit.

Similar differences appear in comparison of the species unit with the unit of total diatoms, the most striking of which concern the shape of the general polygon of distribution (fig. 5). Here the total diatoms polygon shows like peaks of production near its two ends separated from a median lesser peak by two deep depressions. On the contrary, *N. seriata* shows minor peaks near the two ends and a major median peak followed by another only slightly lesser. In addition the manuscript records indicate that *Chaetoceras curvisetum* Cl. competed closely with *N. seriata* through the first two weeks and *Skeletonema costatum* (Grev.) through the rise in abundance near the last of the period.

Apparently, there is shown in this case an interrelationship of fluctuations amongst the diatoms themselves. The first rise of abundance in which one or more other species shared the prominence of *N. seriata* may have marked a sharply competitive period in which several species were trending toward numerical dominance. *N. seriata* may have emerged from this competition in better condition to pass the week of apparent adversity, following which it came up strongly to almost a condition of pure culture. At the time of its final weakening *Skeletonema costatum* happened to be in best condition to take the lead in numbers.

Now it is surely possible that the good catches of sardines and mackerel in the La Jolla region in 1920, already mentioned in this report, may have been closely related to this February abundance of *Nitzschia seriata* Cl. This diatom may be a preferred food for these fishes, or it may have been a better food than they usually get at that season, or it may have been a preferred food for animal plankton used by these fishes. If so, a number of fluctuations in animal species would be closely associated with the fluctuations of the diatom species, and a complete understanding of biological phenomena in that entire year would be impossible without information concerning all of them.

GEOGRAPHIC ORIGIN OF FLUCTUATIONS

For the sake of relative clarity in the paragraphs immediately preceding no comment was made on the problem of geographic relationships of fluctuations, but in the sea these relationships are too important to pass without notice.

It is true that the polygon in figure 5 is too regular in form to suggest any relation to geography or topography but so great regularity in distribution of diatoms is rare.

For present purposes it may suffice to state six postulates concerning geographic relationships: First, that there is a steady drift of water bearing swarms of plankton through a given locality, the thin edge of a swarm approaching first, followed by increasing density to a median maximum, and then by decreasing density toward a minimum. Second, that there is no drift strong enough to carry a swarm through a locality or to displace the resident species. Third, that seasonal, periodic, or irregular currents of great magnitude may carry a swarm into a locality, or take one out, or introduce stimuli favorable to rapid development of organisms already present. Fourth, that minor currents of variable extent and duration may flow into or through a locality, introducing conditions destructive of local dominance or contributory to establishment of such dominance. Fifth, that a locality constitutes a seed bed from which distribution of swarms occurs with more or less regularity in season. Sixth, that exuberant growth may be coincident over an area so large that the general abundance of particular organisms in a median part of the area is not materially affected by water movements of ordinary type.

Without going into detailed discussion of these postulates it may be suggested that the abundance of *Nitzschia seriata* Cl. in February, 1920, might be explained by either the second or sixth; while the "red water" of 1924 (Allen, 1928*b*) seems more likely to be covered by the third or fourth. It is impossible to avoid the supposition that

geographic influences play a prominent part in many cases of fluctuation in numbers of marine organisms, but observational investigation of these influences is extremely difficult on account of the large areas which should be studied simultaneously by different types of investigators.

STATIONS OF DISCONTINUOUS COLLECTING

PACIFIC GROVE

Catches were made daily at Pacific Grove (on Monterey Bay) the first three months and most of the last six months of 1923, and through most of the first six months and the last three months of 1924. In 1923 only one weekly average of diatoms reached the number of six thousand cells to the liter. Few weeks showed an average over one thousand. In 1924 three weeks of the second quarter of the year showed averages exceeding eleven thousand but the numbers were very small through all of the fourth and most of the first quarters. There was no prominent difference between the species listed there and at the southerly stations except that *Fragilaria islandica* Grun. yielded the largest single catches. This species is rarely, if ever, found at La Jolla.

REDONDO

Forty-six catches taken at Redondo (near Los Angeles) July to October in 1921 showed small numbers except for four days, September 29 to October 3, inclusive, in three of which there were more than one hundred thousand cells to the liter. No numbers approaching these in size appeared at any of the regular stations in the last five months of 1921. Since Pt. Hueneme is a little farther north and Oceanside and La Jolla considerably farther south it seems apparent that this conspicuous pulse at this point was due to narrowly localized conditions of some unrecognized origin.

SANTA BARBARA

Through the first three weeks of April, 1921, daily catches were taken at the United States Kelp Experiment Station pier just outside of Santa Barbara. Large numbers of diatoms (averaging over 300,000 cells to the liter) were found there for twelve days, when there was a precipitous drop to small numbers. The productivity in the first week closely resembled that at all of the three regular more southerly stations at the same time. But the decline in numbers after April 12 was earlier than at any of these, although closely followed by Pt.

Hueneme. The sharpness of the decline resembled that of Oceanside and La Jolla a week or two later, indicating a general tendency to sharp reduction over a large area.

Discontinuous catches were made at another pier in Santa Barbara in July, August, November, and December of 1921. Several catches were above ten thousand cells to the liter in mid-July when catches were very small at other stations, but in August there were none nearly so large as at the regular stations. All of the November and December catches were very small, averaging smaller than at the regular stations. The species listed were those commonly found at the other stations.

The discontinuous evidence available indicates that in its characteristics of diatom distribution Santa Barbara differs from the southerly stations less than might be expected. The lower temperatures and greater turbulence of water there lead one to expect marked differences from La Jolla and Oceanside.

REPRESENTATIVE CHARACTER OF PIER CATCHES

No doubt many observers are impressed with the obvious possibility that pier catches do not furnish reliable information concerning conditions offshore where the influence of land is so much less and the influence of the continuous mass of water so much greater. There is no great amount of direct evidence available but there is a considerable amount of inferential evidence obtainable from this five-year period.

The case of "red water" in 1924 (Allen, 1928*b*) yields direct evidence to indicate close resemblance of inshore and offshore conditions at the surface of the sea over a period of two or three weeks. The same streakiness of surface water was visible offshore that was so noticeable near the pier, some catches offshore showed numbers of organisms similar to those in catches at the pier, and the same species were found in numerical dominance in both localities.

As a matter of fact, in several seasons of collecting in the La Jolla region the species found at the surface inshore and offshore at comparable times showed no discernible difference. Fewer comparative collections in other regions indicate similarly close resemblances of the species components of surface catches inshore and offshore..

The evidence concerning numbers is not so clear. Sometimes inshore catches have been heavier than those a few miles offshore. Sometimes the reverse has been true. The general indication of manuscript records for the La Jolla region is that numbers at the pier usually fluctuate coincidentally and within similar ranges with

those two or three miles offshore while numbers at the surface more than five miles offshore are usually smaller and it is probable that fluctuations are usually somewhat different in time although having a general successional resemblance. Wherefore one may conclude that in at least some regions inshore catches give fairly good indications of conditions of development of the phytoplankton in the outlying sea.

LEADING SPECIES OF LEADING GENERA OF DIATOMS

In studying the records I have listed the leading species for five years at the regular stations in three different ways, showing leadership for quarters (table 2), leadership for months (table 3), and occurrence at some time at some station in numbers averaging more than ten thousand cells to the liter for one or more weeks. These lists are very closely similar as to names included (cf. tables 4 and 5), so it is fairly evident that less than twenty-five authentic species deserve mention for prominence in the southern California region. Some of these do not lead with frequency sufficient to warrant giving them individual discussion under present limitations. Partly because of this and partly because I have already given cursory reference to some of them in tables in the section on seasonal differences in species, I shall confine individual discussion to a single species in each of the five most prominent genera.

ASTERIONELLA JAPONICA Cleve

This species is the only representative of the genus *Asterionella* noticed in the pier collections. With individual cells shaped somewhat like an old-fashioned wooden potato masher and joined side by side by the large ends into more or less spirally twisted colonies it has probably been confused in identification less frequently than any other species. It is also less variable than most other species, either in shape or size. As it commonly appears its cells are larger than those of almost all of the species of *Chaetoceras* so prominent amongst plankton diatoms of southern California.

As shown by table 4 it is commonly found at all the regular pier stations and often in considerable numbers. Although maximum abundance for a month was found at Oceanside in 1923 the greatest continuity of representation occurred at Pt. Hueneme in 1924 and the largest number of months in the five years showing averages above one thousand cells to the liter appeared at La Jolla. Apparently the species may thrive at any of these stations in favorable periods but over a period of years Pt. Hueneme seems to be least favorable. At

TABLE 4
FIVE YEARS' DAILY AVERAGE FOR MONTHS

	January	February	March	April	May	June	July	August	September	October	November	December
Pt. Huene	1924 8	48	205	672	196	1,606	558	1,294	616	60	432	25
	1923 17	32		25	23	94	296	1,013	48	112		9
	1922 1921			560	224					50	217	
	1920	114	104	1,149	956	64				57		
Oceanside	1924 1923	1,024	652	8,736		32		24	8	88		134
	1922	675	144	313	10,400	16	20				180	25
	1921	8	8	75				134		8	241	
	1920											
La Jolla	1924	55	2,754	180		211						
	1923	220	384	144	790							1,434
	1922	1,153	1,706		8	1,951			14	3	71	
	1921	22	25	333							60	
	1920	30	113	455	1,036				106			72

both La Jolla and Oceanside the first quarter of the year (table 6) seems to be the most favorable season, but at Pt. Hueneme it is difficult to say whether the second or the third quarter seems to be most favorable.

Although this species rarely appears in catches in numbers as great as one hundred thousand cells to the liter its relatively large size and its tendency to abundance early in the year when other photosynthetic organisms lack abundance entitle it to consideration as one of the important plankton diatoms of southern California waters. If some one should discover that it is extensively used for food by the animal population this characteristic of early abundance would become highly important from ecological considerations on account of providing sustenance in an unfavorable season.

CHAETOCERAS DEBILE Cleve

There is no species of *Chaetoceras* prominent in the southern California region which is not sometimes subject to confusion of identification under the necessary conditions of statistical examination. *Chaetoceras debile* Cl. is probably frequently confused with *C. curvisetum* Cl. and I have recently discovered in Alaskan material that *C. sociale* Lauder may sometimes be involved in this confusion. In southern California material the only recognized difficulty has been in distinguishing the first two. Throughout these series the sole basis of separation has been the rectangular interspace of *C. debile* and the biconvex interspace of *C. curvisetum*. Even if one could induce himself to believe that this is an infallible mark of distinction he may still be frequently baffled by the unfavorable angle at which the chains lie in the counting cell.

On the showing of voluminous manuscript records there is some indication that the two species do not reach maxima at the same time. One sometimes appears to increase as the other decreases. Taking this point at its face value one is tempted to say that they are not similarly responsive to the same environmental conditions. But this inference cannot escape question because it is certainly possible that only one of these species is ever abundant and that the preponderance of numbers with a certain shape of interspace at one time and with a different shape of interspace at another time may be due to environmental influences within a species as well as between two species. It is also possible that in case of small cells and indistinct interspaces the count would tend to be excessive in the direction of the shape most frequently discerned clearly. In spite of these difficulties the distribution of *C. debile* indicated grossly by table 5 seems to have definable features.

In the first place its presence seems to be more nearly constant year by year and month by month at Pt. Hueneme although no month there showed an average so high as that of April at Oceanside in two different years, or so high as that of both April and May at La Jolla in 1922.

There is an apparent tendency toward greatest abundance in April. In five years at two stations and four years at one there were thirteen months with daily averages above ten thousand cells to the liter, six of which fell in April, two in the preceding month, and three in the following month. This evident tendency toward high or maximal abundance in April is in accord with the showing of collections in Alaskan waters in 1923 where some very large numbers were taken in April at several points between Hecate Strait and Yakutat Bay (Allen, 1927c).

Just how nearly representative these features may be of the genus *Chaetoceras* as a group it is impossible to say since no other species record has been examined to even this limited extent of detail. However, the general appearance of the records suggests considerable similarity of other species and this species seems to be more frequently and abundantly represented than any other of its genus in thousands of miles of coastal waters in the eastern Pacific.

In the matter of leadership in monthly averages *C. debile* Cl. is much ahead of any other species of diatoms with a total of twenty months of leadership distributed amongst the three stations in the five years. The catchall group *Chaetoceras* sp. had a total of sixty-nine months of leadership distributed amongst the three stations but its lack of definition makes comparison of this kind impossible.

On its general numerical showing *C. debile* appears to be the most important plankton diatom in the eastern Pacific. Nothing is known, however, concerning its ecological importance, its food value to animals, or the good or evil part played by it in this territory.

EUCAMPIA ZODIACUS Ehrenberg

The genus *Eucampia* is probably represented in southern California coastal waters by two species, *E. groenlandica* Cleve and *E. zodiacus* Ehr. If both are present the former is only rarely observed and the latter is the only really important representative of the genus. The shape and size of the cells of *E. zodiacus* may vary to wide extremes but ordinary variations though numerous are within moderate limits, the proportion of length to breadth, or conversely, not often exceeding two to one. Usually there is little trouble with confusion in identification but some of the very narrow chains are difficult to distinguish from *E. groenlandica* and there are certain

TABLE 6
FIVE YEARS' DAILY AVERAGE FOR MONTHS

	January	February	March	April	May	June	July	August	September	October	November	December
Pt. Hueneeme	1924											
	1923	168	256	5,464	2,594	43,248	11,180	672	2,216	360	730	19
	1922	29 196	145 77	268 3	22,560 133	5,344 71	23,949 79	90 34				
	1921	122	187	1,303								
	1920	55	223	2,769	2,008	1,553	21,574	94	315	92		
Oceanside	1924											
	1923	304	160	652		4,118	40		748	64	16	262
	1922	68	456	38	2,240	829	72		89	328		
	1921	1,718	166	543	68					14	6,757	
	1920			1,197		762	227	1,059				
La Jolla	1924											
	1923	192		25	50	1,311	8		467		40	1,111
	1922	379	901	1,558	964	166	4		38			
	1921	863	268	21,363		801		1,523	11	75	55,173	2
	1920	56	4,382		757		4,477		122	93		

positions of chains of both *E. zodiacus* and some species of *Hemiaulus* which make separation difficult under low magnifications. In most catches the cells of *E. zodiacus* are larger than those of many other plankton diatoms and its numbers are therefore more important than is evident superficially.

My general impression after several years of experience with this species is that it is erratic in distribution and that it has a tendency to form relatively localized swarms. Some evidence of this tendency is shown in table 6 where the seven daily averages above ten thousand for a month are distributed from April to November, appearing in five different months at La Jolla and Pt. Hueneme, mostly at the latter. This table indicates also that it is more characteristic of the Pt. Hueneme region although it is fairly prominent at La Jolla.

Apparently the species may appear at any one of the three stations at any time of year but most commonly in the second and third quarters. The relatively large numbers in November, 1922, at La Jolla is distinctly exceptional although its high average there is due to a well sustained pulse covering the two weeks at the middle of the month. In both the first and last weeks of the month its numbers were small. As indicated by the Oceanside entry in table 6 there was a little indication of a November pulse at that station, but the manuscript details show the increase there to have been of short duration and a week later, in the last week of the month.

There are indications from offshore catches by boat (Allen, 1918b) that this species does better at subsurface levels and possibly at some distance from shore. This may account in part for erratic features of its distribution in surface catches at the piers although it seems to show some of those same characteristics in boat catches. At any rate it has considerable numerical importance and it may have peculiar value for investigation if it really is as erratic in distribution and as narrowly localized in its extremes of abundance as it appears to be. Such characters suggest the possibility that it may have an unusual degree of sensitivity to changes in environmental conditions. If so it may be much easier to trace correlations between its abundance and certain environmental factors than would be the case with a mixed population or a less sensitive species.

NITZSCHIA SERIATA Cleve

The genus *Nitzschia* is probably represented by a number of species in southern California plankton. Of these *N. seriata* Cl. is far the most important. *N. longissima* Ralfs. is common but its numbers are usually small. *N. pungens* Grun. was recorded regularly in 1920 but it was dropped from the lists in the following years because of

TABLE 7
FIVE YEARS' DAILY AVERAGE FOR MONTHS

	January	February	March	April	May	June	July	August	September	October	November	December
Pt. Hueneine	1924 32 1923 928 1922 30 1921 44 1920	40 306 63 221 148	537 1,376 82 209 2,114	1,240 4,768 71 2,760 4,594	1,146 52,280 2,515 1,177 28,265	14,070 168,000 460 323 29,703	3,092 1,062 10,751 264 13,284	5,324 151 3,160 2,460 285	1,861 52 1,486 86 1,177	2,360 288 1,756 123 1,004	176 496	38 12 32 44
Oceanside	1924 95 1923 73 1922 3 1921 1920	1,656 2,689	89 2,704 952 954	40 377 167 6,091	44,692 250	1,024 272 595 87	164 45 29	96 2 3,104	70 198 2 769	224 3,000 30 66	896 28 1,115	326
La Jolla	1924 33 1923 1,128 1922 477 1921 586 1920 340	88 1,488 650 177 94,729	422 1,306 413 378 27,535	22 1,510 496 19,492 1,199	11 46,050 1,722 5,629 25,077	1,249 3,206 2,467 305 51,871	 44 60 72,328	16 16 4 347	70 205 17 804 443	32 24 54 192 47	1,296 33 3,525 38	3,462 182 2 517

confusion with small forms of *N. seriata*. As a matter of fact its presence was never clearly established and in this discussion it is not separated from *N. seriata*. Indeed, one or two other small species having this type of colony formation may be thus included. Larger forms of *Nitzschia* of non-colonial type are probably present at times but none have been satisfactorily distinguished from naviculoid forms. Numerically, *N. seriata* Cl. probably constitutes about ninety per cent of the representation of the genus at the pier stations, volumetrically, probably more than this.

The cells of *N. seriata* vary greatly in size but such differences are rarely, if ever, observable in the same chain. Cells of the most common size have about the same volume as those of the larger forms of *Chaetoceras*. The shape varies from almost linear to that of a rather thick spindle. The chains differ considerably in appearance, due mainly to the fact that in some chains the cells are joined by the extreme tips, while in others they are in contact through about one-third of their length. In spite of all of these differences the species is usually easy to recognize under low magnification.

On the basis of leadership in averages for months, *N. seriata* was second only to *Chaetoceras debile* Cl. in the five years of pier collecting. Average daily production for the five years was about five thousand cells per liter as against about six thousand cells per liter for *C. debile*. Since the cells of *N. seriata* may average about twenty per cent greater in volume than those of *C. debile* it is possible that the volumetric production of the two species for the five years is not essentially different.

According to table 7 Oceanside was distinctly less favorable than the other two stations for *N. seriata*. Only once in the four years of collecting there did the daily average for a month get as high as ten thousand cells per liter while in seven months it was greater than that at each of the other stations. However, five of these at La Jolla and three at Pt. Hueneme came in 1920 before collecting was begun at Oceanside. The prominence of the species at both of these stations in that year gives reason for thinking that Oceanside, in an intermediate location, might have been also favorable at that time. The close similarity of its numbers at all three stations in May, 1923 (table 7) gives strong indication of it. But there is still a general appearance of lighter production at Oceanside over the four-year period. This might be due to greater inflow of fresh water from streams closer to Oceanside, a condition which this species might not be able to tolerate. In the last two years of the five-year period, table 7 shows Pt. Hueneme to be distinctly more favorable than the other two stations.

The seasonal distribution was essentially similar at all three stations, maximal abundance coming mainly in the second quarter, but there is some indication of a tendency to increase earlier at La Jolla, a little later at Oceanside, and a little later still at Pt. Hueneme. However, with the exception of the peculiar pulse in February, 1920, at La Jolla (already mentioned in discussion of fluctuations) the greater abundance in every year at all stations has been in the second quarter. On the other hand the species has been recorded in every month of the year at all three stations and some of the records for weeks indicate that it may show considerable abundance at almost any time. Because of continuity of representation as well as because of abundance *N. seriata* is certainly one of the most important diatoms in the southern California territory.

SKELETONEMA COSTATUM (Grev.)

Only one species of the genus *Skeletonema* has been observed in the plankton of the eastern Pacific. *S. costatum* is widely distributed but it seems to thrive best in more northerly waters. Although it is sometimes found in great numbers in southern California there has been no catch to equal one of more than a million cells per liter near Duke Island in Southern Alaska in 1923. The larger numbers and more nearly constant representation at Pt. Hueneme through the five years also indicate more favorable conditions northward. The fact that table 8 shows greatest abundance at La Jolla and Oceanside to be in the first quarter of the year while the second quarter is shown to be most favorable at Pt. Hueneme gives some reason for thinking that the rising temperatures of the second quarter at the southerly stations may have considerable inhibiting effect. That temperature may have a strong influence is also suggested by the showing that this species was represented with exceptional continuity through most of the year at Pt. Hueneme in 1924 when the temperature rose less than in other years.

Although the cells of *S. costatum* vary considerably in size and shape they have not been found larger than those of *Chaetoceras debile* Cl. Numerically and volumetrically the species is probably less important than *C. curvisetum* Cl. or *C. compressum* Lauder, especially in the Gulf of Santa Catalina. However, its prominence is sufficient to bring the genus *Skeletonema* within the leading five at southern California piers, and it has made at different times substantial contributions to the diatom populations in this region.

TABLE 8
FIVE YEARS' DAILY AVERAGE FOR MONTHS

	January	February	March	April	May	June	July	August	September	October	November	December
Pt. Hueneme	1924		102	6,392	314	2,398	1,350	4,530	3,045	338	32	
	1923	48	6,328	166	816	1,088	614	248				
	1922	165	276	2,321	1,769	22	4,175	6,511	96			25
	1921		751	21,937	595	272	114					
	1920		282	9,494	1,296	1,113						
Oceanside	1924		45			205		248	32	152	224	25
	1923	255	9,807	153	1,328	192	64	28				
	1922	223	10			243	2			2	266	3
	1921		1,037	1,112							194	
La Jolla	1924		114			123						
	1923	1,516	7,950	912				404	228			
	1922	355	266	168	61	244	2		12	20	1,366	3
	1921	394	2,209	1,473		624			891			
	1920	165	735	63	511							223

SPECIES OF DIATOMS NEVER ABUNDANT

The following list gives the names of species often recorded in southern California pier catches but never in the five years reaching a daily average of five hundred cells per liter for a week. Some of these have been found in greater abundance in other regions or off-shore and at subsurface levels in southern California. Excellent examples of this are *Chaetoceras criophilum* Castr., *C. neapolitanum* Schr., and *Thalassiothrix frauenfeldii* (Grun.). It is evident therefore that conditions at piers are ordinarily unfavorable for many species. A few species on this list are fairly common in the eastern Pacific but they have been few wherever found. They seem to have a high degree of tolerance for various conditions but a small degree of responsive sensitivity to favorable conditions. *Planktoniella sol* (Wall.) is an excellent example.

Actinopterychus splendens (Ehr.)
Actinopterychus undulatus (Bail.)
Asteromphalus heptactis (Breb.)
Asteromphalus hookeri Ehr.
Bacteriastrum elongatum Cl.
Biddulphia aurita (Lyngb.)
Biddulphia extensa Mann
Biddulphia mobiliensis (Bail.)
Cerataulina bergonii Perag.
Chaetoceras criophilum Castr.
Chaetoceras gracile Sch.
Chaetoceras neapolitanum Schr.
Chaetoceras pendulum Karst.
Chaetoceras tetrastichon Cl.
Chaetoceras simile Cl.
Coscinosira polychorda (Gran.)
Ditylum brightwellii (West)
Grammatophora marina (Lyngb.)
Lauderia borealis Gran.
Licmophora lyngbyei (Kütz.)
Lithodesmium undulatum Ehr.
Planktoniella sol (Wall.)
Rhizosolenia alata Btw.
Rhizosolenia calcar avis Schu.
Rhizosolenia faeroensis Ostf.
Rhizosolenia robusta Norm.
Rhizosolenia setigera Btw.
Stephanopyxis turris (Grev.)
Thalassiothrix frauenfeldii (Grun.)
Thalassiothrix longissima Cl. and Grun.

Several species of the following genera have also been noted with considerable frequency but usually in small numbers. *Achnanthes*, *Actinocyclus*, *Climacodium*, *Cocconeis*, *Coscinodiscus*, *Nitzschia*, and *Surirella*.

TABLE 9
DINOFLAGELLATE DAILY AVERAGES BY MONTHS

	January	February	March	April	May	June	July	August	September	October	November	December	
Pt. Hueneme	1924	208	520	371	752	2,996	2,435	9,996	6,184	3,741	3,280	1,312	510
	1923	140	264	580	1,995	1,110	4,800	10,759	2,288	2,429	1,184	132	957
	1922	30	66	108	805	392	406	6,447	4,394	4,032	21,865	1,208	262
	1921	67	67	240	427	1,196	1,203	1,054	558	1,677	312	97	48
	1920		486	390	1,376	6,120	5,956	9,217	21,334	2,555	1,714	343	130
Oceanside	1924	496	888	1,286	2,584	12,144	35,821	1,430	1,648	1,294	1,400	2,720	717
	1923	242	282	3,040	4,586	6,990	7,172	537	440	470	656	1,064	403
	1922	378	23	616	4,165	20,631	7,613	356	352	251	228	2,007	192
	1921		335	624	1,268	899	1,245	871	728	1,076	1,231	467	377
	1920												
La Jolla	1924	539	605	810	2,123	10,627	24,256	688	616	1,425	938	2,472	922
	1923	408	550	788	1,949	5,110	4,000	729	696	962	402	3,165	2,785
	1922	479	342	786	4,161	5,243	2,736	637	460	757	906	1,366	607
	1921	855	356	766	2,996	927	1,558	709	519	1,075	882	493	427
	1920	539	3,845	5,958	1,337	8,463	8,589	1,869	2,758	2,076	1,214	1,452	1,605

DINOFLAGELLATES

In actual numbers produced at the regular pier stations the whole group of Dinoflagellates was distinctly inferior to several single species of diatoms, compared either by single years or for the five-year period. But, since single cells of most of the armored dinoflagellates are larger than nearly all diatom cells, and especially cells of the leading species of diatoms, their value as links in the food chains of the sea may often compare favorably with that of the diatoms.

The general characteristics of distribution of the two groups are similar in the fact that they tend to increase markedly in numbers in the second quarter of the year. At La Jolla and Oceanside piers this increase led to maxima of dinoflagellates in the second quarter of every year but at Pt. Hueneme maxima were not reached until the third quarter, in 1922 not until the last quarter (table 9). This lag in rise of numbers of dinoflagellates is similar to the lag in rise of temperature of the sea water at Pt. Hueneme and suggests a demonstrable influence of rising temperature in favor of productivity. Stated in terms of months the difference in the appearance of maxima at the three stations is even more evident than it is in terms of quarters. La Jolla and Oceanside had maximal production in June, April, May, May and June, and June, distinctly within the second quarter in every case. Pt. Hueneme had maximal production in August, September, October, July, and July, just as distinctly in the third quarter or later. Changing more slowly than at the southerly stations, temperatures (fig. 2) sometimes rise at Pt. Hueneme until October, whereas the maximum is nearly reached at La Jolla and Oceanside by July or in August. Like that of the diatoms the abundance of dinoflagellates shows considerable difference in different years at all three stations. On account of the much smaller numbers involved these differences have very limited range as compared with those of the diatoms. Still they are large enough to show definitely that 1921 was a poor year at all three stations, that 1923 was rather poor at La Jolla and Oceanside, that 1920 and 1922 were relatively very good at Pt. Hueneme, that 1924 was the best year at La Jolla and Oceanside, that Pt. Hueneme led in total abundance in three out of five years, and that Oceanside was second in total abundance twice and first in total abundance once in its four years.

LEADING SPECIES OF DINOFLAGELLATES

A cursory examination of the manuscript records of distribution of dinoflagellates through the five years indicates that *Prorocentrum micans* Ehr. was most frequently the leader in numerical prominence of considerable significance. It also had the appearance of greater constancy of representation than any other species. In size it is much smaller than several species of the genus *Peridinium* and some species of *Gonyaulax*, *Ceratium*, and *Dinophysis*. It is slightly smaller than the smallest species of these genera ordinarily observed in southern California. On the other hand it is considerably larger than cells of most of the common species of diatoms. Studies in progress by Mr. H. M. Buley at the Scripps Institution at the time of this writing indicate that it is extensively used as food by mussels (*Mytilus californianus* Conrad) and this may be regarded as direct evidence that it has an important place in the food chains of this region. It appears to tend to greatest abundance at the piers in June or July.

The necessary limits of this paper forbid such detailed examination of the records as is required to establish satisfactorily the order of numerical prominence of other species of dinoflagellates. *Ceratium tripos* (O. F. M.) appears to be the leading species of the genus which probably had the lead in total numbers. *Ceratium furca* (Ehr.) and *C. fusus* (Ehr.) have been observed with frequency in most years, sometimes in considerable numbers.

On account of the large size of some common representatives of the genus *Peridinium* (e.g. *P. divergens* Ehr. and *P. depressum* Bail.) coupled with occasional large numbers of smaller species such as *P. minutum* Kof. it is possible that this genus was nearly, if not entirely, in the lead in volumetric production.

The genus *Dinophysis* is almost continuously represented in southern California pier collections, most prominently by *D. caudata* Kent (or closely allied species) but it is rarely represented by large numbers or great volume.

So far as the five-year period is concerned the foregoing statement is also true of the genus *Gonyaulax* (*G. polyedra* Stein most prominent) but outbreaks of "red water" referred to in the discussion of 1924 material in the report for that year (Allen, MS) show that it has great powers of development at times.

PHYSICAL AND CHEMICAL CONDITIONS

Chemical studies have been carried on only at the pier of the Scripps Institution. For the five-year period ending with 1924 they had not been sufficiently developed to give much assistance in discussing the general environment for a report of this character. Therefore, no attempt will be made to discuss relationships of chemical conditions to abundance of diatoms and dinoflagellates.

Temperature and salinity are the physical conditions which have been under particular observation at the piers for many years. Even at the surface level of these inshore stations there has been no study of the distribution of physiologically effective light to the organisms in the water, and no continuity of attention to such subsidiary conditions as land drainage into the sea, and viscosity.

SUNSHINE

Concerning light there is a little crude information available for La Jolla pier through the records of percentage of sunshine by the U. S. Weather Bureau at San Diego (U. S. Weather Bureau, 1921-1925; see fig. 2) supplemented by field records at La Jolla pier. Of course this tells nothing concerning the amount and character of usable light available for diatoms even a foot below the surface of the water, but it does give a rough basis of comparison of atmospheric light of different years and of months of different years not too far from one of the pier stations. Sunshine records at San Diego show a range of monthly totals extending from forty-six per cent to eighty-nine per cent of what is possible if every day of the month should be entirely clear. The lowest amount (46%) was for February, 1920, the February most productive of diatoms of any in the five years (fig. 2). Increase of sunshine in March and April was accompanied by decrease of diatoms to a relatively low average of numbers for April but a decrease of sunshine to fifty per cent in May was accompanied by the highest average of diatoms for the year. Here was a distinct negative correlation which reached its end in August with minimum production of diatoms accompanying almost a maximum of sunshine. In 1921 conditions were almost exactly conflicting in regard to diatom maxima because maximum sunshine for the year in April (79%) accompanied an abundance of diatoms almost maximum whereas the true maximum of diatoms in June appeared with almost a minimum percentage (56%) of sunshine. The maximum

of diatoms in April, 1922 came with almost a minimum (68%) of sunshine, although the maximum (87%) of sunshine in November was accompanied by a strong increase of diatoms. Median percentage (77%) of sunshine in May, 1923 accompanied the maximum of diatoms. In 1924, the poorest year for diatoms, the percentage of sunshine in January (89%) was highest of any month for the five years except that of November, 1923, which equaled it. Maximum numbers of diatoms came in November, 1924 with a median percentage (72%) of sunshine.

The general indication of these diatom maxima and submaxima is strongly in the direction of negative correlation between abundance of diatoms and sunshine, a surprising condition in view of the common assumption that increase of sunshine, especially in the first quarter of the year, should favor increase of diatoms. Other observers, notably at the Millport Station in Scotland (Scottish Marine Biological Association Annual Report, 1926-27) have commented on the deleterious effects of too much sunlight and have recorded examples of negative correlation somewhat resembling these. In the more southerly location of southern California it should be expected that deterrent effects of too much sunlight or too nearly vertical rays of the sun would be more often observable or more strongly evident than in the Millport region. From such considerations the negative correlation does not appear surprising.

RAINFALL

When discussing greater or less abundance of sunshine in southern California one is reminded of one of its negative correlatives, rainfall. This factor is itself a complex or inseparable associate of a number of chemical and physical factors which have never been even separated, much less studied. However, the rainfall composite has nothing of moment to contribute to the solution of the problem associated with variations in abundance of sunshine, for out of five times in the five years when the total rainfall for a month reached as high as two inches there was only one month in which such increase in rainfall accompanied a strong increase in numbers of diatoms, and that was in February, 1920. Evidently one cannot properly conclude that because both rainfall and abundance of diatoms show negative correlation to abundance of sunshine they must be in positive correlation to each other.

SALINITY

Although salinity is regularly discussed as a physical factor of marine environment it must be evident that in our present state of knowledge it is very difficult to distinguish between the physical effects of salinity in the sea and the effect of any of the multitude of substances which contribute to salinity. From ten years of acquaintance with marine plankton and observation of its ranges of tolerance of conditions which it must meet, I have formed the opinion that the physical differences in salinity of typical sea waters are not sufficiently great to be significant in interpreting phytoplankton distribution.

However, something of interest is observable concerning these relationships in the five years' period. Most obvious is the showing of manuscript records for days and weeks which indicate (especially at Oceanside, where a stream enters about a mile from the pier) that a heavy inflow of fresh water was followed for some time by almost complete absence of diatoms and dinoflagellates. But since these extreme reductions always occurred at a time of very light production of these organisms there is some room for doubt as to the absolute character of the deterrent influence throughout the general locality.

Concerning records at periods more productive of diatoms it may be noted that salinity was about median (about 33.5‰ through the highly productive February of 1920 and that it was somewhat above this (about 33.7‰) through the very lightly productive first quarter of 1924 at La Jolla. Contrary to this the heavy production at Pt. Hueneme in 1924 was in a salinity still a little higher (about 33.9‰). The small numbers of diatoms indicated for the end of 1921 and the beginning of 1922 at all three stations seem to be definitely related to heavy rains and marked reduction in salinity. Apparently one may safely conclude that wide ranges in salinity may show recognizable influence on the phytoplankton but that ordinary changes do not.

TEMPERATURE

The general situation regarding temperature is somewhat like that of salinity. Of course temperature is not a composite factor but its combination of direct and indirect influences renders it almost, if not fully, as difficult as if it were. In the southern California region it is probable that temperatures at the surface are never so low as to be directly deterrent to development of plankton organisms. The simplest indication of this probability lies in the occurrence of large and vigorous populations offshore at subsurface levels where minimum

temperatures of the year for the surface (13°C) are the ordinary temperatures of midsummer. Concerning higher temperatures there is more probability of direct injury. The simplest indication of this is the fairly common sloughing off and killing back to some feet below the surface, of the kelps along the southern California coast in hot weather. In some of its aspects this phenomenon resembles "sun scalding" of land plants in hot weather. Some of the bad effects may be due to unusual penetration of injurious light rays but since the kelp seems to thrive well enough through periods of intense light so long as the water stays below a certain temperature the direct relation of temperature seems fairly certain. Obviously, if this relation is true of the kelp it is likely to be true of the plankton organisms accustomed to meeting the same range of conditions. Several features of these relationships in the natural environment deserve the scrutiny of physiologists as well as that of ecologists.

At La Jolla the only prominent indications of relation of temperature to abundance of diatoms appear in the first quarters of 1920 and 1924. In 1920 the temperature for the first quarter was mostly about 14°C while in 1924 it was mostly about 15°C . At Pt. Hueneme the first quarters of these two years were much alike, both keeping fairly close to 14°C or a little below. As already stated in other connections 1920 was good at La Jolla and poor at Pt. Hueneme in the first quarter while the reverse was true in 1924. With such conflict of evidence in the cases most favorable for such comparison it is evident that the exact nature of influence of usual ranges of temperature cannot be clearly traced.

GENERAL SUMMARY

Most of this paper is a highly condensed (triply or quadruply) statement from which many points of interest have been omitted and in which some points have been discussed with reference to manuscript records too extensive to be included. Selection of points for discussion and of material for inclusion has mainly been based on regard for the needs and interests of the work in California localities. Some outstanding features may be designated as follows:

1. There is considerable variability in annual production of plankton organisms in the southern California region in general and in some localities in particular.

2. Localities not only differ in total production of diatoms and dinoflagellates from year to year and for five years, but they also differ in seasonal distribution of these organisms in particular years, La Jolla and Oceanside being more nearly like each other than either is like Pt. Hueneme.

3. In total numbers of both diatoms and dinoflagellates for aggregate periods of five and four years Pt. Hueneme was superior to both La Jolla and Oceanside. But it should be noted that in case of the diatoms this superiority is due to reversal from leadership of La Jolla in the first two years of the five to leadership of Pt. Hueneme in the last two years of the five.

4. In most years at La Jolla, Oceanside, and Pt. Hueneme the second quarter was most productive of diatoms. But the first quarter showed greatest numbers at Pt. Hueneme in 1921 and Oceanside in 1923, and the last quarter had largest numbers at La Jolla in 1924.

5. Detailed analysis of one series of fluctuations indicated that time units not larger than the day are necessary if one would prevent erroneous interpretations of some records of distribution of organisms.

6. Five genera contributed the leading species of diatoms at the regular stations for the five years. The leading species of dinoflagellates were comprised in three genera.

7. A negative correlation of maximal abundance of diatoms and maximal abundance of sunshine is indicated.

8. Within ordinary ranges in typical sea water there is (in the southern California region) no indication of direct influence of salinity and temperature upon changes in abundance of diatoms and dinoflagellates.



Fig. 1. Map to show general geographic relations of principal stations.

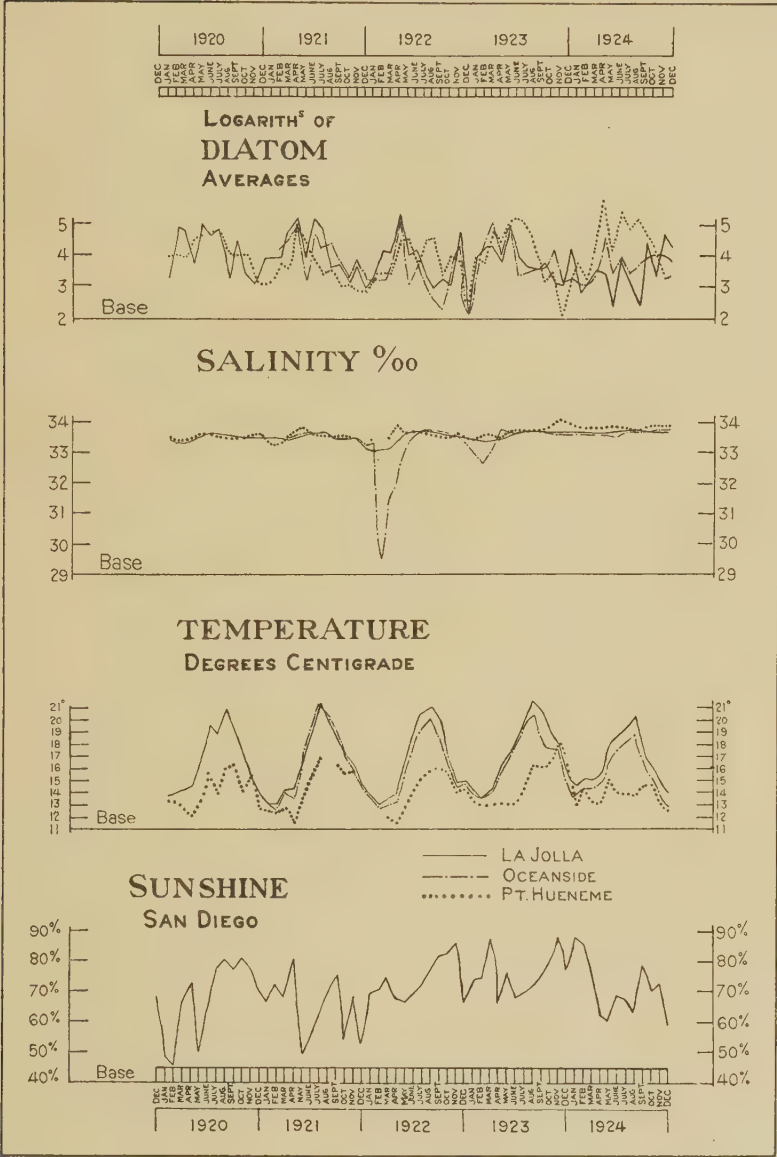


Fig. 2. Graphs to show distribution by months through successive years of diatoms (logarithms of average numbers to liter), salinities, temperatures, and sunshine (at San Diego).

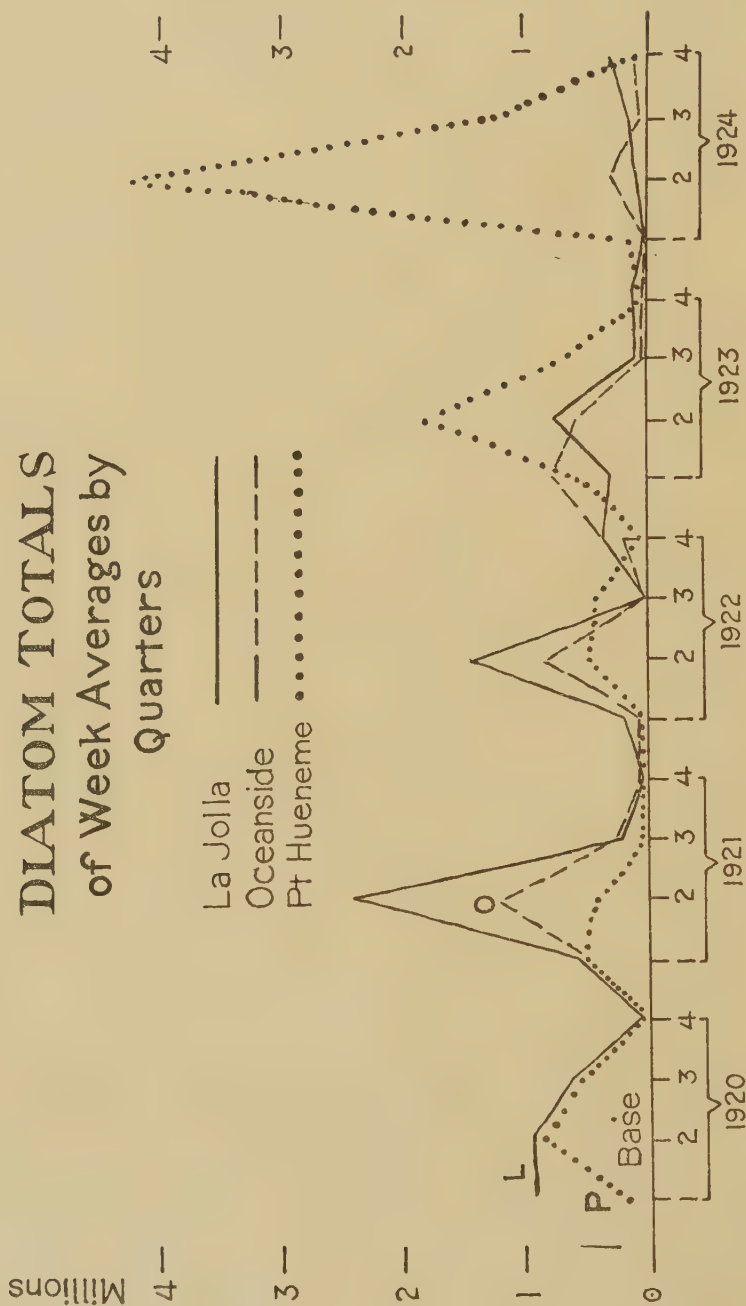


Fig. 3

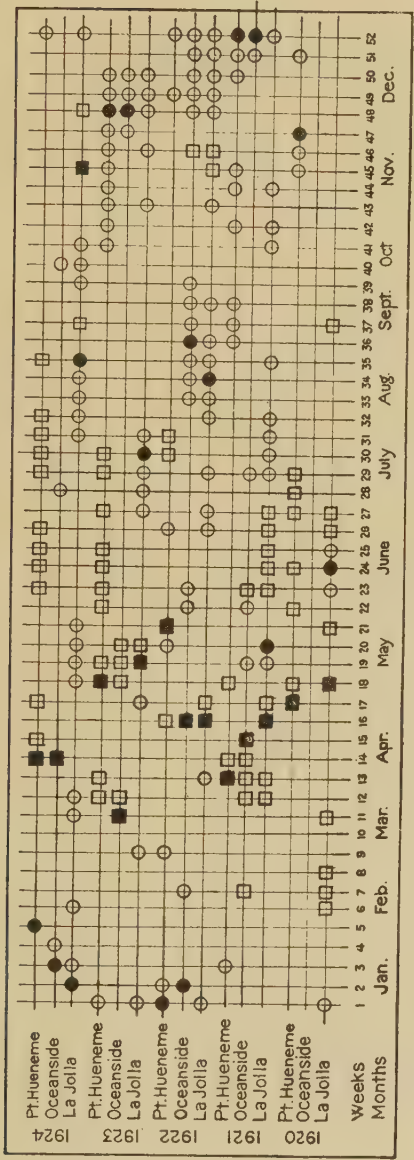


Fig. 4. Graph to show weeks averaging below 500 diatom cells to liter, over 100,000 cells to liter, and lowest and highest weeks in five successive years at two piers and four years at one pier. Hollow squares show weeks above 100,000. Solid squares show weeks having highest average. Hollow circles show weeks below 500. Solid circles show weeks having smallest average.

NITZSCHIA SERIATA CI.

At La Jolla Pier

Feb. 1920 to

Mar. 17, 1920

Cells to
Liter

Total Diatoms A.M. ---
Nitzschia } P.M. —○—
seriata } A.M. —

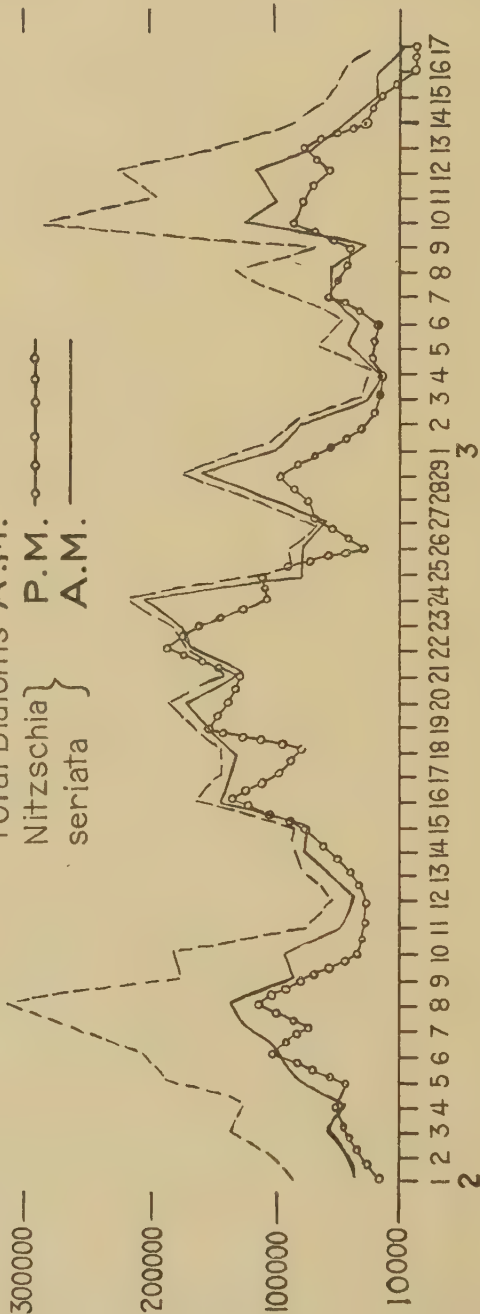


Fig. 5

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